Preliminary Investigations on Insects Affecting the Reproductive Stage of the Silversword (Argyroxiphium Sandwicense DC.) Compositae, Haleakala Crater, Maui, Hawaii

Herbert K. Kobayashi
University of Hawaii
Honolulu, Hawaii

Haleakala's silversword (*Argyroxiphium sandwicense* DC.), a member of the Composite family, reproduces almost exclusively from seed; therefore the flowering-to-seedling stages are crucial in its life cycle as in any typical seed plant (Pelton 1953). After germination and juvenile growth governed by a particular set of edaphic constraints, the silversword usually remains unaffected by disease or physical damage under natural conditions until a terminal inflorescence of about 100 floral heads appears and ends a life of 7 to 20 years (Kobayashi 1973).

The objective of my research was to assess the effect of insects on the number of seeds available for germination in the field as part of a four-year study on the ecology of the silversword (Kobayashi 1973). Vandalism, browsing, and insect larval damage to developing seeds were believed to be the main causes of silversword decline during the past several decades (Degener 1930; Bryan 1948; Carlquist 1970).

Materials and Methods

All fieldwork was done on the seedcrop of 1971; no flowering occurred during 1970, and only one plant bloomed in 1972.

To assess the number of viable seeds available in the absence of insect damage, 10 mature heads were randomly selected intact from each of all plants found to be apparently free of damage when inspected with a 10x hand lens. All 206 plants that flowered in 1971 were visited, and only three isolated late-blooming plants could pass inspection (see Fig. 1 for location). Each head was divided into three concentric zones of equal area and the number of damaged and undamaged seeds counted under a dissecting microscope. Viability was determined directly by dissecting each undamaged seed and noting the presence or absence of a spindle-shaped embryo completely filling the seedcoat. A count of the fly puparia found was made for each zone.

To assess the number of viable seeds available for dispersal, 100 mature heads were randomly chosen from each of 12 populations subjectively selected to cover a wide range of field conditions (see Fig. 1 and Table 1 for locations). Insect damage was estimated by eye for each head, and 10 heads from each location dissected for the presence of embryos.

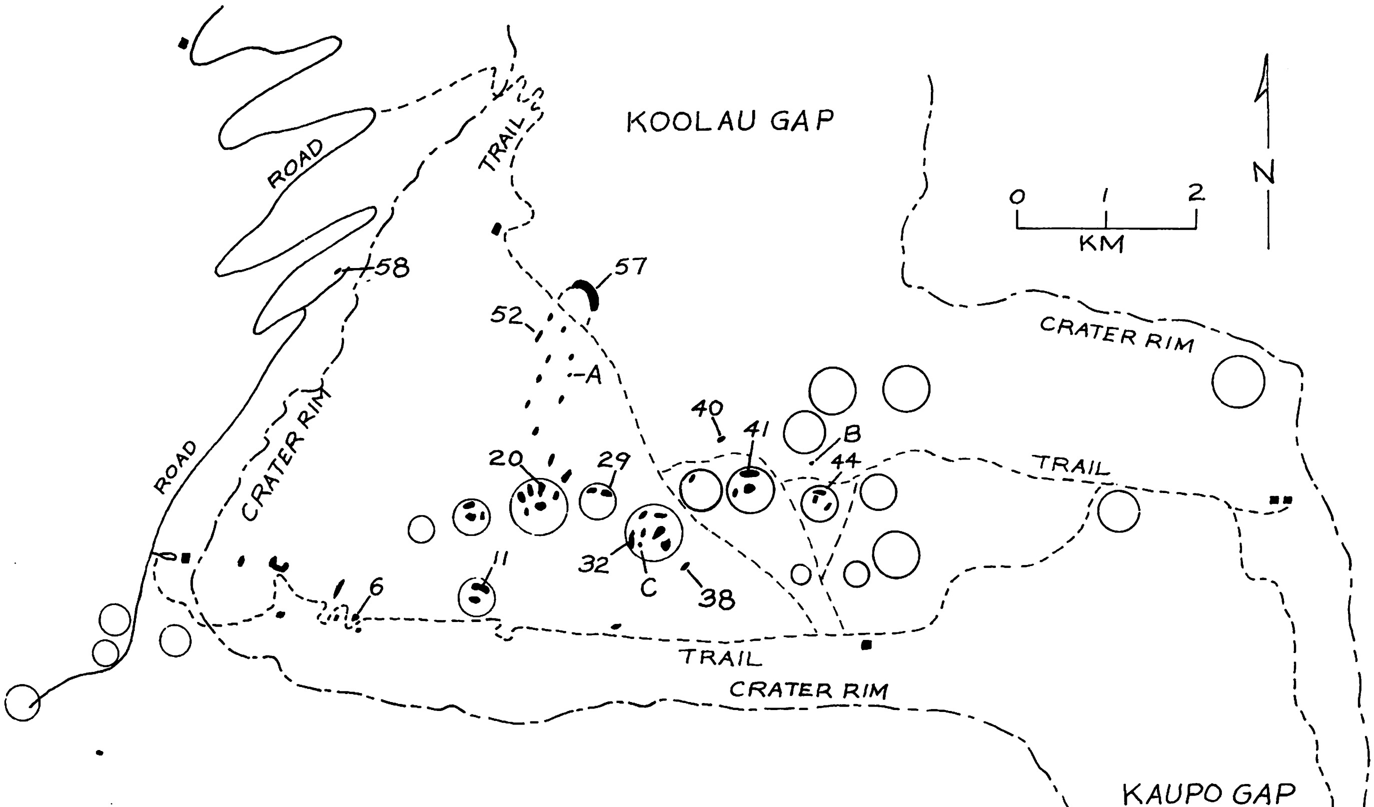

FIG. 1. Map of Haleakala Crater showing all silversword populations with 25 or more plants. Circles are cinder cones. Numbers and letters are explained in Tables 1 & 2.

Results and Discussion

Pollination. Table 1 presents presumptive evidence that *A. sandwicense* is cross-pollinated: as much as half of the heads randomly selected from a plant may contain no embryos. Since florets are at various stages of maturity within a head and among heads within an inflorescence, ample pollen is available during flowering for self-pollination if the plant is capable of doing so. Such a high percentage of empty seeds (typical of several composite genera) may be the result of sporophytic incompatibility within isolated populations on Haleakala (personal communication from Dr. J.L. Brewbaker, Dept. of Horticulture, Univ. of Hawaii).

Cross-pollination by flying insects is indicated by the comparison of viability of undamaged seeds in Table 1 (4 to 7%) and Table 2 (26%), a difference significant at the 99% confidence level. Table 1 seeds are from isolated individuals that bloomed off-season when fewer flying insects were seen, whereas Table 2 seeds were collected soon after the active summer season. A possible pollinator is *Nesoprosopis* (=*Hylaeus*) *volcanica* (Perkins). During the summers of 1969 and 1971, this endemic bee was found on every bloom, actively ingesting pollen. *N. volcanica* was not among the insects listed for *A. sandwicense* by Swezey (1954). No other insect could be directly connected with pollination by the author.

Larval Damage to Seeds. Over a hundred years ago, Hillebrand (1854) reported that seeds of *A. sandwicense* and *A. virescens* (found only on Haleakala) were "... generally destroyed by insects." Since then, nearly every general description of the silverswords have viewed this natural ecological factor with alarm despite the findings of the only

TABLE 1. Number and location of viable seeds in the floral heads of 3 plants almost free of insect damage 1972

	Plant Designation (see Fig. 1)		
	A	*B*	*C*
Date 10 heads collected	Feb. 23	Apr. 5	Feb. 22
Pct. heads with no viable seeds	50%	20%	0%
Avg. diameter of head	2.8 cm	2.0 cm	3.6 cm
Avg. number of seeds per head	298	271	342
Avg. number of viable seeds in concentric zones (see text):			
Zone 1, central	1	0	2
Zone 2, medial	4	8	4
Zone 3, peripheral	6	10	11
Total per head:	11	18	17
Avg. no. of damaged seeds per head*	3	2	3
Avg. no. of puparia per head*	1	1	2

*Damaged seeds and puparia found only in Zone 1, all heads.

field study of silversword insect infestation which concluded that "... if the plants can be protected from other types of vandalism I believe that they will be able to survive the insects" (Lamb 1936). The following three points based on my preliminary work support Lamb, and show that more field data are needed to properly assess the larval damage to seeds.

The first point is that larval damage to seeds is a natural ecological factor present long before the coming of man. The most destructive insects are the larvae of *Rhynchephestia rhabdotis* Hampson and *Tephritis cratericola* Grimshaw which feed on the developing seeds of blooming plants (Swezey and Degener 1928, Degener 1930, Lamb 1935b). Although Swezey (1954) found these insects only on *A. sandwicense*, *T. cratericola* was found on another *Argyroxiphium* species and *R. rhabdotis* possibly on the closely related Dubautias (personal communication, Dr. D.E. Hardy, Univ. of Hawaii). Through coevolution the insects probably depend on the survival of sufficient seeds to avert extinction of their plant hosts; therefore great damage to seeds is not necessarily detrimental to the existence of the silversword. However long-term studies are needed to evaluate any disturbance introduced by non-native organisms into this natural relationship.

The second point (a corollary to the first) is that while examining hundreds of heads in every flowering population of the 1969 and 1971

TABLE 2. Insect damage and seed viability for 12 selected populations 1971

	*Population designation and location**	*Number of plants*	*Number flowered 1969*	*Number flowered 1971*	*% seeds damaged by insects*	*% viability of undamaged seeds*
6	Sliding Sands Trail	240	12	2	50	21
11	Puu-o-Pele cone	2,190	9	8	90	39
20	Puu-o-Maui cone	7,600	4	1	80	31
29	Un-named cones	1,750	5	23	90	38
32	Ka-Moa-o-Pele cone	370	3	2	70	35
38	Ka-Moa-o-Pele outlier	50	0	1	20	19
40	Near 8" rain gauge	360	4	3	10	18
41	Puu Naue cone	950	6	16	70	26
44	Puu Nole cone	1,720	6	8	70	24
52	Red aa flow	30	1	2	20	16
57	Silversword Loop	430	20	25	60	22
58	Kalahaku Overlook	150	13	3	70	28
	Total	15,840	83 (Total)	94 (Total)	60 (Mean)	26 (Mean)

*See Fig. 1 for Approx. locations. Designations are as listed in Appendix III, Kobayashi 1973.

seasons, none were found with seeds completely destroyed by insects, thus raising the possibility that seeds are always available despite heavy infestation. According to Table 2, the most heavily damaged population (pop. 29) still had at least 3% of its total seedcrop available for dispersal at the end of the 1971 flowering season. Viable seeds survive because the insects generally attack only the inner disc seeds of the floral head and leave the outer disc and ray seeds intact. In particular, the peripheral ray seeds numbering up to 20 are protected by the fibrous bracts characteristic of the tarweed subtribe Madinae (Carlquist 1959), and are highly fertile compared to the inner disc seeds (compare Zones 1 and 2 with 3 in Table 1). When collecting seeds in the field, the last point is important because the bracts which may contain as much as 50% of the viable seeds in a head are usually discarded by laymen as well as botanists. Collecting technique may account for the wide disparity in the percent viability of seeds reported by earlier investigators.

The last point to consider is the relationship between the extent of damage and population size: generally large populations suffer most while small isolated ones are the least damaged (Table 2). Since the large populations have remained large on the relatively undisturbed cinder cones and red flows of the crater floor for the past 100 years (Alexander 1870, Lamb 1935a, Powers 1938, Anonymous 1945, Badaracco 1962), high infestation does not necessarily lead to a drop in number. Even if the plants are reduced to "... barely a hundred specimens ..." as in 1927 (Degener 1930), a number disputed by Lamb (1936), small isolated populations may act as nuclei for the reestablishment of large populations.

Flowering. The number of flowering plants preseason on Haleakala may vary from zero (personally observed in 1971) to 815 in 1941. and also varies considerably from year-to-year and place-to-place among the populations (Table 2). The number of blooming plants and the extent of insect damage in a population were not found to be statistically correlated in any manner. The question of whether a non-flowering season reduces the number of larvae and thence decreases the extent of insect damage is not known. This can be answered by laboratory experiments or by repeating the work of Table 2 during a good flowering season which has been preceded by a non-flowering one.

Acknowledgments

The author wishes to thank the Hawaii Natural History Association for the individual research grant supporting this work. Dr. Wallace C. Mitchell, Chairman of the Dept. of Entomology, Univ. of Hawaii, and Mr. Ralph Harris, former Park Naturalist, Haleakala National Park gave valuable advice and encouragement.

REFERENCES CITED

Alexander, W.P. 1870. On the crater of Haleakala, Island of Maui, Hawaiian Group. Am. J. Sci. 49(145): 43-48.

Anonymous. 1945. Silverswords no longer threatened with extinction. Honolulu Advertiser Newspaper. Oct. 28, 1945.

Badaracco, R. 1962. Report of silversword census and status. Haleakala National Park, National Park Service.

Bryan, L.W. 1948. Ahinahina, the unique silversword. Paradise of the Pacific Magazine 60(12): 40 and 125.

Carlquist, S. 1959. Studies on Madinae: anatomy, cytology, and evolutionary relationships. Aliso 4(2): 171-236.

______. 1970. Hawaii, a natural history. Natural History Press, New York, 463 p.

Degener, O. 1930. Ferns and flowering plants of Hawaii National Park. Star-Bulletin Press, Honolulu. 312 p.

Hillebrand, W.F. 1854. Report on the standing committee on floriculture. 4th annual meeting. Transactions of the Royal Agricultural Society 2(1): 110-113.

Kobayashi, H.K. 1973. Ecology of the silversword *Argyroxiphium sandwicense* DC. (Compositae) Haleakala Crater, Hawaii. Ph.D. Thesis. Univ. of Hawaii 91 p.

Lamb, S.H. 1935a. First progress report silversword project. March 3, 1935. Haleakala National Park.

______. 1935b. Second progress report silversword project. July 1935. Haleakala National Park.

______. 1936. Final progress report. The 1935 silversword project. January 1936. Haleakala National Park.

Pelton, J.F. 1953. Ecological life cycle of seed plants. Ecology 34: 619-662.

Powers, H.A. 1938. Progress report on investigation of silversword in Haleakala Section, Hawaii National Park. Haleakala National Park.

Swezey, O.H. 1954. Forest entomology in Hawaii. B.P. Bishop Mus. Spec. Pub. 44. 266 p.

Swezey, O.H. and O. Degener. 1928. Insect fauna of the silversword and greensword. Proc. Hawaiian Entomol. Soc. 7(1): 183-185.